Nitrogen transfer between N₂-fixing plant and non-N₂-fixing plant

JIANG San-nai(蒋三乃)*, ZHAI Ming-pu(翟明普)

(College of Resource and Environment, P.O. Box 189, Beijing Forestry University, Beijing 100083, P. R. China)

Abstract: The transfer mechanisms, calculating methods and ecological significance of nitrogen transfer between legumes and non-legumes are briefly reviewed. There are three pathways of nitrogen transfer from legumes to neighboring non-legumes: (1) the nitrogen pass in soluble form from the donor legume root into the soil solution, move by diffusion or/and mass flow to the receiver root and be taken up by the latter; (2) nitrogen pass into the soil solution as before, be taken up and transported by mycorrhizal hyphae attached to the receiver roots; (3) if mycorrhizal hyphae form connections (bridges) between the two root systems, the nitrogen could pass into the fungus within the donor root and be transported into the receiver root without ever being in the soil solution. The mechanisms of nitrogen transfer between N₂-fixing plants and non-N₂-fixing plants are reviewed in terms of indirect and direct pathways. The indirect N-transfer process is related to the release of nitrogen from legumes (donor plants), the possible interaction of this nitrogen with soil, the decomposition and mineralization of legumes and turnover of nitrogen, the nitrogen absorbing and competing abilities of the legume and the non-legume (receiver plant). The direct nitrogen transfer process is generally considered to be related to the nitrogen gradient and physiological imbalance between legumes and non-legumes, and when the donor legume lies in stressful stage (i.e. removal of shoots or attacked by insects), the nitrogen transfer can be improved significantly. The methods of determining nitrogen transfer (indirect ^{15}N-isotope dilution method and direct ^{15}N determination method) are evaluated, and their advantages and shortcomings are shown in this review.

Key word: Nitrogen transfer; N₂-fixing plant; Non-N₂-fixing plant

Introduction

Nitrogen is an element that cycles through an ecosystem and needs to be present at a certain minimum level to sustain that system. In an interspecies context, the beneficial effects of N₂-fixing plants in ecosystems, due to their contribution of nitrogen, have been observed by succeeding generations of agronomists, foresters, and ecologists. The inter-plants of N₂-fixing plants and non-N₂-fixing plants are practiced to increase total yield and reduce the need for fertilizers input, and it has been shown that part of the assimilated N in the non-N₂-fixing plants originated from the legume partners in such inter-cropping systems (Giller et al. 1991; Haystead et al. 1988; Ledgard & Steele 1992; Stern 1993; Jensen 1996; Johansen & Jensen 1996; M ärtensson et al. 1998). Various species of legumes has been used for centuries in crop rotations and other kinds of in-

ter-planting systems such as species-mixed forest plantations. Theoretically, inter-planting systems combining N₂-fixing plants and non-N₂-fixing plants should offer certain opportunities to maintain the system in a positive nitrogen balance, primarily through the input of atmospheric nitrogen via the legume-rhizobia symbiosis and then this symbiotically fixed N being transformed into several forms as follow: (1) Some of them can be taken up and transported within the legume and assimilated; (2) some of them can be released and lost from the legume, and be made available to inter-cropped plants, or incorporated into the soil organic matter (SOM); and (3) under certain circumstances, some of them may be transferred directly to the inter-planted non-N₂-fixing plants.

Transfer of nitrogen is the movement of nitrogen from a legume to another plant, either during growth of an interplant association with a legume component, or as residual nitrogen for the benefit to a succeeding plant. Utilization of nitrogen by the non-legume in an inter-planting community with legume depends on the amount of legume residue, the manner and rate of decomposition of this residue, and on what conditions prevail to permit transfer from the legume to the non-legume. Estimates of nitrogen transfer from a legume to a companion non-legume range between

25 and 155 kg $\cdot$ hm^{-2} $\cdot$ a^{-1} (Stern 1993).

Nitrogen transfer between N_2-fixing plant and non-N_2-fixing plant involves several processes, and the better understanding of these processes can further use the beneficial effects of legume in farming and forest ecosystems. However, up to date, the processes concerning nitrogen transfer are not well understood, even though many individual studies are documented in some detail. The brief review here is to assess the role of nitrogen transfer in inter-planting systems that consist of N_2-fixing plants and non-N_2-fixing plants and to summarize the advances of studies on the mechanisms of nitrogen transfer among such systems.

Pathways of nitrogen transfer

The flow of nitrogen between legumes and non-legumes in inter-planting communities has been proposed to occur mainly below ground by three different ways:

Firstly, the N_2-fixing plant may release nitrogen into the soil through decomposition and mineralization of litters and dead roots (Hart et al. 1997; Giardina et al. 1995; Ineson & McTiernan 1992; Briones & Ineson, 1996), exudation of roots (Fan 1994). This nitrogen may be reabsorbed by the legume entering the internal nutrient cycling or taken up by non-legume species growing nearby (Ledgard & Steele 1992). It's generally considered that in inter-planted associations turnover of nitrogen in roots and nodule debris of legume is the major source of transferable nitrogen (Laidlaw et al. 1996). Legume rhizo-deposits consist of sloughed and dead root materials with high N concentration and root exudation that contain more amino-N than non-legume (Fan 1994). The continuous and enhanced turnover of legume roots (especially fine roots) resulting in rhizo-deposits of low C-to-N ratio indicate that nitrogen transfer from the legume to a connected non-legume is most likely. The rapid decomposition and mineralization of litters of legumes may increase the concentration and availability of nitrogen in the soil, since most of nitrogen nutrient in the soil can move readily for a relative long distance by means of mass flow or/and diffusion. This increased available nitrogen may be transferred to the rhizosphere of non-legume in an inter-planting system and taken up by the non-legume. This is an indirect N-transfer route from N_2-fixing plant to non- N_2-fixing plant, and this process runs slowly because it is related to the long-termed biogeochemical process.

Secondly, as described as before, in the course of decomposition, mineralization of litters, dead roots, nodule debris and sloughed cells of legumes, and because of the excretion of legume roots, which contains high N concentration, the content and availability of nitrogen of the soil are improved. In the inter-planting systems of N_2-fixing plants and non-N_2-fixing plants, if roots of non-legumes are infected by mycorrhizal fungus, the external hyphae or strains of mycorrhizae may uptake this nitrogen nutrient and transport them into the neighboring non-legumes (receiver plants) through their particular nutrient translocation channels (Read et al. 1985; Stern 1993; Veirheilig et al. 1998; Jensen 1996; Frey & Schuepp 1993). This is also an indirect transfer pathway because the nitrogen provided by N_2-fixing plants is transported through soil solution.

Thirdly, in legume and non-legume communities, the nitrogen fixed by legumes is transferred directly to the non-legumes through mycorrhizal hyphal bridges, which commonly connect roots of N_2-fixing plants (donor plants) and non- N_2-fixing plants (receiver plants). In such a case, nitrogen is transferred from legumes to non-legumes without entering the soil solution. A reduction in the amount of symbiotically fixed N released into the soil solution will increase the efficiency with which the fixed N is utilized (Martensson et al. 1998). Mycelial networks (or bridges) connecting two or more plants, belonging to the same or different species, have been directly observed in transparent observation root chambers (Heap & Newman 1980; Chiariello et al. 1982; Ikram et al. 1994). Furthermore, it has been demonstrated that mycorrhizal links can provide pathway for carbon and nitrogen transfer between plants (Finlay & Read 1986; Arnebrant et al. 1993). Read et al. (1985) suggested that transfer of nutrients from established plants to seedlings may be a crucial factor enabling young plants to survive in nutrient-limited situation. Newman (1988) summarized several possible benefits of a seedling becoming connected to an already established mycelial network (bridge). Other experiments have also reported that mycorrhizal hyphae connecting roots of legume and non-legume mediate the below-ground transfer of nitrogen (e.g. Hamel & Smith 1991; Frey & Schuepp 1993; Jensen 1996; Johansen & Jensen 1996; Tomm et al. 1994; Martensson et al. 1998; EK et al. 1996).

Mechanisms of nitrogen transfer

Although many findings have shown that nitrogen transfer occur between N_2-fixing plants and non-N_2-fixing plants in associated ecosystems, the mechanisms of N-transfer among them have not been clearly understood so far.

Indirect nitrogen transfer

For the indirect nitrogen transfer pathways (including the first and second pathways described

above), or say soil pool pathways, the mechanism is generally considered to be related to the "sink-pool" theory. Above- and below-ground parts of N_2-fixing plants contain higher nitrogen concentration and lower C-to-N ratio compared with non-N_2-fixing plants. When litters, dead roots, sloughed cells and nodule debris are decomposed (earlier studies showed that litters and dead components of legumes may be decayed and mineralized rapidly because of their lower C-to-N ratio (e.g. Giardina et al. 1995; Briones & Ineson 1996), more nitrogen is released into the soil solution and the nitrogen input to the soil is increased by the legume's N_2-fixing process. On the other hand, roots of legumes may excrete N compounds into the rhizosphere, which contain more amino-N materials. The role of active excretion by legume is unclear, but it has been reported that the exudation of some amino acid is an important factor for the proliferation of rhizobium and also increase the size and activity of the microbial biomass in the rhizosphere, which in turn may increase the availability of other nutrients (Jensen 1996). Significant amounts of C and N are deposited in the rhizosphere of legumes during growth season (Whipps 1990; Fan 1994; Jensen 1996). So, rich nitrogen pool is formed in the rhizosphere of N_2-fixing plants and distinct nitrogen concentration gradient occurs between the root zone of legume and non-legume in an inter-planting system, especially under nitrogen-limited circumstances. The N deposited may be reabsorbed by the legume itself, or by an associated non-N_2-fixing plant after it has been released by mineralization and transported into the absorbing vicinity of roots or mycelial hyphal networks of the latter (VA mycorrhizal hyphae are known to play a role in the uptake of NH_4^+ from soil and its translocation to the host plant (Johansen et al. 1991)). This enable the neighboring non-N_2-fixing partners to uptake more nitrogen from the soil pool than they absorb under conditions of sole planting. Particularly, when N_2-fixing plants are inter-cropped with N-catch plants, for example Chicory (*Cichorium intybus* L.), which has been proved to be an efficient scavenger of soil N (Karlsson-Strese et al. 1996), the amount and efficiency of nitrogen transferred from the former to the latter may be significantly improved.

However, up to date, the mechanism of indirect nitrogen transform has yet to be clarified. Whether nitrogen is transported by means of diffusion or mass flow is still unclear. By and large, the importance and quantity of legume nitrogen in the N-nutrient of an inter-planted community depend on: (1) the effect of rhizo-deposits on the minerlization-immobilization turnover of nitrogen in the soil, (2) the competition for plant-available soil nitrogen between legume and associated non-legume, (3) the capacity for N-uptake in the associated non- N_2-fixing plant, and (4) the

availability of other soil sources, for instance, some free-living organisms, i.e. the diazotrophs (eg. Azolla), are capable of contributing nitrogen to some ecosystems. Other study by Jensen (1996) showed that nitrogen transfer indirectly from N_2-fixing plant to non- N_2-fixing plant can also be enhanced by increasing the number of root contacts between the inter-cropped plants.

Direct nitrogen transfer

There have been many studies reporting direct nitrogen transfer between legume and non-legume and much attention is paid to this question so far. (e.g. Heap & Newman 1980; Francis et al. 1986; Newman 1988; Hamel & Smith 1991; Frey & Schuepp 1993; Johanson & Jensen 1996; Olsson et al. 1998; Vierheilig et al. 1998; Laidlaw et al,1996; Hamel et al. 1992; Haystead et al. 1988). It has been proved that many species of mycorthizal fungus may infect a wide range of host plant species and their external hyphae or strains can extend for several centimeters and form networks in the soil. When these external haphas or strains met roots of another plant species, the latter is likely to be infected and so mycorrhizal bridges (networks) between roots of different plants are formed.

These hyphal bridges (or networks) between roots of different plants have been observed by many workers, for example, Heap and Newman (1980), using the buried agar-covered microscope slides technique, found that mycorrhizal external hyphal connections existed between different roots of one plant species *Lolium perenne* L and also between roots of two different plant species *L. perenne* L and *Plantago lanceolata* L (These two species are commonly found together in permanent pasture). Similar observations on other plants also show that hyphal connection between roots of the same and different plant species are possible (Read et al. 1985; Chiariello et al. 1982). If mycorrhizal connections between roots of different plants occur to any large extend, then it may be possible for nutrients to pass between the roots connected, especially, when N_2-fixing plant is inter-cropped with non- N_2-fixing plant in the same plot, and these two different plants are infected by common mycorrhizae.

Though large numbers of studies on the structure and function of mycorrhizal roots have been carried out, relatively little attention has been given to the mycelial phase of the symbiosis in the soil. The main reason is probably that while entire mycorrhizal roots or even root systems can readily be extracted from soil with little damage, it is extremely difficult to carry out a non-destructive investigation of the mycelial systems. Advanced technology and equipment should be provided to solve these questions.

Nevertheless, the significance of the external mycelia for nutrition of individual plants with mycorrhizal has been demonstrated. For instance, the result of experiment by Chiariello et al. (1982) showed that Vesicular-Arbuscular mycorrhizae connects the root systems of different plant species in a serpentine annual grassland and probably mediate nutrient transfer among them. Frey and Schuepp (1993) reported that roots of berseem (Trifolium alexandrinum) and non-legumes (maize and apple) can be associated via the haphae of VAM fungi (Glomus intracadices), and by using ^{15}N as tracer, 4.7% of the ^{15}N transferred to mycorrhizal maize was derived from berseem. The quantity of nitrogen transferred between various associations of plant species is different and is depended on physiological properties of these plant species or other unknown factors. Study by Johansen and Jensen (1996) also showed that roots of pea (Pisum sativum) and barley (Hordeum Vulgare L.) can be linked by external hyphae of Glomus intraradices and when removing the shoots of pea (donor plant), 15% of the donor-root (Pea) nitrogen is transferred to the receiver plant (barley). Martensson et al. (1998) reported that, in the inter-crop systems combining N_2-fixing plants (peas and clovers) and non-N_2-fixing plants (genetic varieties of chicory, a specie of nitrogen scavenger, demonstrated as above), the percentage of nitrogen in the varieties of Chicory derived from transfer from neighboring intact legumes ranges between 3% and 50%, and that by removing the shoots of legumes, 3, 4.5, 6 months later, the percentage of nitrogen in the varieties of chicory derived from transfer ranges from 15% to 18%, 46% to 77%, and 20% to 34%, respectively. Similar conclusions have been drawn in other studies (Hamel et al. 1991a, 1991b, 1992; Haystead et al. 1988; Jensen 1996).

Removal or shading of donor shoots was imposed to force a higher transfer of nutrients to receiver plants. The transfer of N was particularly enhanced by removal of the legume donor shoots, since greater amount of nitrogen was lost from dying roots of legume and the possibilities for improving nitrogen transfer from N_2-fixing plants to non-N_2-fixing plants occur. Johansen and Jensen (1993) demonstrated that the percentage of donor-root nitrogen transferred to the receiver plant (barley) ranged from no significant transfer, in non-mycorrhizal controls with living donor plants (peas), up to about 15% in the mycorrhizal treatments with donor-plant shoots removal. Experiments by Ikram et al. (1994) and by Giller et al. (1991) suggest that it is possible to increase the mycorrhizal-mediated transfer of legume nitrogen to non-N_2-fixing plants through shoots removal and insect attack, respectively. Nitrogen transfer to barley from peas could also be signifi-

cantly improved by harvesting the peas, which forced a rapid turnover of donor plant roots (Johansen & Jensen 1996). Up to 60% of total root nitrogen of Lolium perenne were lost three weeks from detached roots, however, when interconnected with non-legume by mycorrhizal bridges, the transfer of nitrogen from Lolium perenne to nearby non-legume plants was increased highly and the loss of nitrogen from the dead roots of the legume reduced significantly (Eason 1988).

All these findings described above support the hypothesis provided by Newman (1988) that, for nutrients transfer, the role of mycorrhizal bridges between living plants is likely to be smaller but it is greater for nutrients transferred from dead donor roots to living receiver plants, since during the processes of donor roots' decomposition, the shoots of donor plants may not compete with roots for nutrients absorbed by mycorthizal hyphae and removal of shoots from the donor plants would have resulted in higher rate of root turnover. So, the intensity of dead donor roots as nutrient source/pool is improved greatly and this is beneficial for nutrients to be transferred from the donor plant (especially legume) to the receiver plant (especially non-legume). Conclusively, the direct nitrogen transfer between legumes and non-legumes depends on the physiological differences among them, creating a source-sink relationship. This physiological imbalance drives the hyphal transfer of nitrogen between them.

Methods of determining nitrogen transfer

The quantification of nitrogen-transfer from a N_2-fixing plant to an inter-planted non- N_2-fixing plant is rather difficult, since the amount of N transferred to the receiver may be small compared to the amount of N taken up from other sources. To estimate the amount of nitrogen-transfer in associations of legume and non-legume, it is necessary to use ^{15}N as a tracer. The ^{15}N isotopic technique can be used in either of two ways: indirect ^{15}N isotopic dilution method and direct ^{15}N determination method.

With the indirect ^{15}N isotopic dilution method, the soil inorganic N pool is labeled with ^{15}N, and by comparing the ^{15}N-enrichments of the non-legume grown in the inter-plant and pure stand situations an estimate of the transfer of N can be obtained. This method is based on the assumption that the same proportion of total N and fixed N in the donor is transferred (Ta & Faris 1987). This method has been adopted to quantify nitrogen transfer in many inter-plants, e.g. of pea and non-legumes (Waterer et al. 1994; Jensen 1996). However, it has severe limitations, especially under field conditions. Firstly, the resolution of the method is low, since the amount of

N transferred from the donor, being mainly non-labeled fixed N, is smaller compared to the amount of ^{15}N-labeled soil N taken up by the receiver plant. Secondly, the root depth and pattern of N-uptake of the receiver plant may be different in the inter-crop and pure stand situations, which may cause the ratio of unlabeled-to-labeled soil N to be different in the two planting situations.

The better method to quantify the contribution of N from legumes to an associated non-legume is direct ^{15}N-isotope determination, since any tracer, incorporated in the legume and detected in the non-legume receiver, is conclusive evidence for transfer. Donor legumes are labeled either by root ^{15}N-labeling (Ta et al. 1989), by foliar labeling (Ledgard et al. 1985; Giller et al. 1991), by stem labeling (Hamel & Smith, 1991), by transplanting labeled plants into soil with receiver plants (Tomm et al. 1994) or by split-root labeling of the legume donor (Ikram et al. 1994). However, a problem exists by using this direct method, it is that the donor plant is usually not labeled uniformly since the tracer is supplied to parts of the roots or the shoots. The supplied, labeled nutrient is then retranslocated throughout the root system of the donor legume. This probably gives rise to concentration differences in different nitrogen pools of the roots, especially if the labeling period is short. Since the relative contribution of the uneven pools of labeled nutrient to the nutrient transfer is unknown, estimates of nitrogen transfer may be misleading. To resolve this problem, extending the labeling period and using a continuous labeling procedure may be useful, just as was done in study by Martensson et al. (1998), they found that a somewhat more uniform distribution of the labeled nutrient could be achieved by this treatment of labeling.

Ecological significance of nitrogen transfer

Legumes are important in mixed planting. A key factor is the input of nitrogen from N_2-fixing plant by means of the Legume-Rhizobium symbiosis. Many reports have documented that non-legumes can benefit from nitrogen supplied by inter-planted legumes (Ledgard et al. 1985; Stern 1993; Haystead et al. 1988; Jensen 1996; Martensson et al. 1998). This process is mainly realized through nitrogen transfer (indirect or/and direct pathways) from N_2-fixing plant, and it plays an important role in stressful environment such as nitrogen-limited soil especially (Frey & Schuepp 1993; Francisco et al. 1996). However, Nitrogen transfer between living legumes and non-legumes is proved to be little significant (Johansen & Jensen 1996; Jensen 1996; Frey & Schuepp 1993), and conflicting reports on the role of direct nitrogen transfer between living plants exist in

literature (Giller et al. 1991; Hamel et al. 1991a; Frey & Schuepp 1993). It has been shown that the amount of nitrogen transferred from dead donor legumes to living non-legume receiver plants is significant (Hamel et al. 1991b; Johansen & Jensen 1996; Martensson et al. 1998). The major ecological role of nitrogen transfer in inter-planted systems may be to improve the uptake efficiency of root systems, to reduce nutrient losses from the soil-plant system, and to partly avoid the mobilization of nutrients by other components of the soil ecosystem such as micro-organism. Nevertheless, so far, the role of nitrogen transfer between N_2-fixing plant and non-N_2-fixing plant is not clearly understood and evaluated, and several problems exist in this research field.

All in all, several processes are involved in the transfer of nitrogen from the legume to the neighboring non-legume. These include the release of nitrogen from the legume plant, the possible interaction of this nitrogen with soil, the residence time of the nitrogen in the soil organic matter or in the soil, and whether it is taken up directly by the companion non-N_2-fixing plant (Stern 1993). Furthermore, because the field situation may be quite complex, further studies are required to be able to analysis extend of nitrogen transfer in inter-planting systems, in different environments and under different forms of management, for the purpose of maximizing nitrogen benefits in interplant systems.

References

Arnebrant, K., EK H., Finlay, R. D., Soderstrom. 1993. Nitrogen translocation between Alnus glutinosa (L.) Gaertn seedlings inoculated with Frankia sp. and Pinus contorta Dong ex Loul seedlings connected by a common ectomycorrhizal mycelium [J]. New Phytol., 124: 231~242.

Briones, M.T.I., Ineson, P. 1996. Decomposition of eucalyptus leaves in litter mixtures [J]. Soil Biol. Biochem., 28(10/11): 1381~1388.

Chiariello, N., Hickman, J.C., Mooney, H.A. 1982. Endomycorrhizal role for inter-specific transfer of phosphorus in a community of annual plants [J]. Science, 217: 941~943.

Eason, W.R. 1988. The cycling of phosphorus from dying roots including the role of mycorrhizas [D]. PhD thesis. University of Bristol.

Fan Jungang. 1994. Biochemical compositions in rhizospheric soil of Robinia psrudoacacia and Sophora japonica and their influence on nutrition of associated poplar [J]. Chinese Journal of Applied Ecology, 5(4): 349~354.

Finlay, R.D., Read, D.J. 1986. The structure and function of the vegetative mycelium of ectomycorrhizal plants. I. Translocation of ^{14}C-labeled carbon between plants interconnected by a common mycelium [J]. New Phytol., 106: 143~156.

Francis, R., Finlay, R.D., Read, D.J. 1986. Vesicu-

lar-arbuscular mycorrhiza in natural vegetation systems. IV. Transfer of nutrients in inter- and intra-specific combinations of host plant [J]. New Phytol., **102**: 103~111.

Francisco, I.P., Peter, H., Juan, P. 1996. Facilitation between higher plant species in a semiaried environment [J]. Ecology, **77**(5): 1420~1426.

Frey, B., Schuepp, H. 1993. A role of vesicular-arbuscular (VA) mycorrhizal fungi in facilitating inter-plant nitrogen transfer [J]. Soil Biol. Biochem., **25**: 651~658.

Giardina, C.P., Huffman, S., Binkley, D., Caldwell, B.A. 1995. Alders increase soil phosphorus availability in a Douglas-fir plantation [J]. Can. J. For. Res. **25**: 1652~1657.

Giller, K.E., Ormesher, J., Awah, F.M. 1991. Nitrogen transfer from Phaseolus bean to inter-cropped maize measured using ^{15}N-enrichment and ^{15}N-isotope dilution methods [J]. Soil Biol. Biochem., **23**: 339~346.

Hamel, C., Smith, D. L. 1991. Inter-specific N-transfer and plant development in a mycorrhizal field-grown mixture [J]. Soil Biol. Biochem., **23**: 661~665.

Hamel, C., Barrantes-Cartin, U., Furlan, V., Smith, D.L. 1991a. Endomycorrhizal fungi in nitrogen transfer from soybean to maize [J]. Plant and Soil, **138**: 33~40.

Hamel, C., Barrantes-Cartin, U., Furlan, V., Smith, D. L. 1991b. Endomycorrhizal fungal species mediate 15N transfer from soybean to maize in non-fumigated soil [J]. Plant and Soil, **138**: 41~47.

Hamel, C., Furlan, V., Smith, D.L. 1992. Mycorrhizal effects on inter-specific plant competition and nitrogen transfer in legume-grass mixtures [J]. Crop Science, **32**, 991~996

Hart, S.C., Binkley, D., Perry, D.A. 1997. Influence of red alder on soil nitrogen transformations in two conifer forests of contrasting productivity [J]. Soil Biol. Biochem., **29**: 1111~1123.

Haystead, A., Malajczuk, N., Grove, T.S. 1988. Underground transfer of nitrogen between pasture plants infected with vesicular- arbuscular mycorrhizal fungi [J]. New Phytol., **108**: 417~423.

Heap, A.J., Newman, E.I. 1980. Links between roots by hyphae of vesicular-arbuscular mycorrhizas [J]. New Phytol., **85**: 169~171.

Heap, A.J., Newman, E.I. 1980. The influence of vesicular-arbuscular mycorrhizas on phosphorus transfer between plants. New Phytol., **85**: 173~179.

Ikram, A., Jensen, E.S., Jakobson, I. 1994. No significance transfer of N and P from Pueraris phaseooides to Hevea brasiliensis via hyphal links of arbuscular mycorrhiza [J]. Soil Biol. Biochem., **26**: 1541~1547.

Ineson, P., McTiernan, K.B. 1992. Decomposition of foliar litter mixtures: a microcosm experiment [M]. In: Responses of Forest Ecosystems to Environmental Changes (A. Teller, P. Mathy and J. N. R. Jeffers, Eds.) pp703~706. Elsevier Applied Science, Barking.

Jensen, E. 1996. Barley uptake of N deposited in the rhizosphere of associated field pea [J]. Soil Biol. Biochem., **28**: 159~168.

Johanson, A., Jakobson, I., Jensen, E.S. 1991. Nitrogen transfer and depletion of soil nitrogen by external hyphae of VA mycorrhizas [C]. Abstract. 3rd European Symposium on mycorrhizas, Sheffield, U. K. 19~23

Johansen, A., Jensen, E.S. 1993. Hyphal transport and transfer of N and P from live or decomposing root of two plants interconnected by a VA-mycorrhizal fungus [C]. Abstract of 9th North American Conference on Mycorrhizae, 8~12 August, 1992. Guelph, Onterio.

Johansen, A., Jensen, E.S. 1996. Transfer of N and P from intact or decomposing roots of pea to barley interconnected by an arbuscular mucorrhizal fungus [J]. Soil Biol. Biochem., **28**: 73~81.

Karlsson-Srese, E.M., Umaerus, M., Rydberg, I. 1996. Strategy for catch crop development. I. Hypothetical ideotype and screening of species [J]. Acta Agric. Scand. Sect. B, **46**: 106~111.

Laidlaw, A.S., Christie, P., Lee, H.W. 1996. Effect of white clover cultivar on apparent transfer of nitrogen from clover to grass and estimation of relative turnover rates of nitrogen in roots [J]. Plant and Soil, **179**: 243~253.

Ledgard, S.F., Steele, K.W. 1992. Biological nitrogen fixation in mixed legume/grass pastures [J]. Plant and Soil **141**: 137~153.

Martensson, A.M., Rydberg, I., Vestberg, M. 1998. Potential to improve transfer of N in inter-cropped systems by optimizing host-endophyte combinations [J]. Plant and Soil, **205**: 57~66.

Newman, E.I. 1988. Mycorrhizal links between plants: their functioning and ecological significance [J]. Adv. Ecol. Res., **18**: 243~270.

Olsson, P.A., Francis, R., Read, D.J., Soderstrom. 1998. Growth of arbuscular mycorrhizal mycelium in calcareous dune sand and its interaction with other soil microorganisms as estimated by measurement of specific fatty acids [J]. Plant and Soil, **201**: 9~16

Read, D.J., Francis, R., Finlay, R.D. 1985. Mycorrhizal mycelial and nutrient cycling in plant communities [M]. In: Ecological Interactions in Soil: Plant, Microbes and Animals (A. H. Fitter, D. Atkinson, D. J. Read, M. B. Usher Eds.). pp 193~217. British Ecological Society Special Publication No. 4. Blackwell Scientific Publications, Oxford.

Stern, W.R. 1993. Nitrogen fixation and transfer in inter-crop systems [J[. Field Crops Res., **34**: 335~356.

Ta, T.C., Faris, M.A. 1987. Species variation in the fixation and transfer of nitrogen from legumes to associated grass[J]. Plant and Soil, **98**: 265~274.

Ta, T.C., Faris, M.A., MacDowall, F.D.H. 1989. Evaluation of ^{15}N methods to measure nitrogen transfer from alfalfa to companion timothy [J]. Plant and Soil, **114**: 243~247

Tomm, G.O., Van Kessel, C., Slinkard, A.E. 1994. Bi-directional transfer of nitrogen between alfalfa and bromegrass: short and long term evidence [J]. Plant and Soil, **164**: 77~86.

Vierheilig, H., AH-Hug, M., Engel-Streitwolf, R., Mader, P., Wiemken, A. 1998. Studies on the attractional effect of root exudates on hyphal growth of an arbuscular mycorrhizal fungus in a soil compartment-membrane system [J]. Plant and Soil, **203**: 137~144

Waterer, J.G., Vessey, J.K., Stobbe, E.H., Soper, R.J. 1994. Yield and symbiotic nitrogen fixation in a pea-mustard intercrop as influenced by N fertilizer addition [J]. Soil Biol. Biochem., **26**: 447~453.

Whipps, J.M. 1990. C Economy [M]. In: The Rhizosphere (J. M. Lynch, Ed.), pp 59~97. Wiley, Chichester.